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Author(s): William H. Romme and Dennis H. Knight

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FIRE FREQUENCY AND SUBALPINE FOREST SUCCESSION ALONG A TOPOGRAPHIC GRADIENT IN WYOMING¹

WILLIAM H. ROMME² AND DENNIS H. KNIGHT

Department of Botany, University of Wyoming, Laramie, Wyoming 82071 USA

Abstract. Differences in fire frequency and the rate of secondary succession following fire have had a major effect on the present composition of forest vegetation in a 4500-ha undisturbed watershed in the subalpine zone of the Medicine Bow Mountains, southeastern Wyoming, USA. Periodic fire coupled with slow secondary succession has perpetuated lodgepole pine forest on the upland, while mature Engelmann spruce-subalpine fir forests have developed in sheltered ravines and valley bottoms where fire is less frequent and succession following fire is more rapid and/or more direct. A graphic model is presented showing the relationship between topographic position, fire-free interval, and the occurrence of mature forests dominated by spruce and fir.

Key words: *Abies lasiocarpa*; dendrochronology; fire; Medicine Bow Mountains; *Picea engelmannii*; Rocky Mountains; *Pinus contorta*; succession; Wyoming.

INTRODUCTION

A forest-type map prepared by the United States Forest Service (1977) for a 4500-ha undisturbed subalpine watershed in the Medicine Bow Mountains of southeastern Wyoming (Fig. 1) shows that spruce-fir forest (*Picea engelmannii* Parry ex Engelm. and *Abies lasiocarpa* [Hook.] Nutt.) is restricted almost entirely to ravines and valley bottoms, whereas slopes and ridgetops are covered by nearly unbroken lodgepole pine forests (*Pinus contorta* Dougl. ex Loud. ssp. *latifolia* [Engelm.] Critchfield). Spruce-fir forest is the presumed climax in much of the area (Daubenmire 1943, Stahelin 1943), and indeed the pine forest frequently has a spruce- and fir-dominated understory. Nevertheless, mature spruce-fir forest is rare on the upland. A similar pattern has been described elsewhere; the interpretation usually given is that the forests along drainages are older due to less frequent disturbance by fire or other perturbations. Habeck (1970, 1976) describes centuries-old red cedar and mixed conifer forests along streams surrounded by younger communities in the Northern Rockies, and Quirk and Sykes (1971) describe stringers of 200-yr-old white spruce forest along ravines in an area of Alaska which is otherwise covered on the upland by a birch-spruce subclimax that usually burns every 40–60 yr. Loope and Gruell (1973) report that lower-elevation spruce forests in northwestern Wyoming are found primarily on sheltered sites that appear to burn less frequently than surrounding areas. Both Clements (1910) and Larsen (1925) describe patches of living trees in western valley bottoms which escaped severe fires that had destroyed the forest on adjacent slopes.

Although differences in fire frequency may be an

important mechanism causing this distribution pattern, another explanation must be considered, namely that more rapid secondary succession following fires on mesic sites permits earlier reestablishment of the spruce-fir climax. Whipple and Dix (1979) observed in northern Colorado that spruce and fir become reestablished after disturbance on drainage bottom sites without the pine-dominated seral stage that characterizes succession on upland sites. Such direct succession (or regrowth), plus the more rapid growth of trees on moist sites, could allow mature spruce-fir forest to develop in less time along drainages than on adjacent uplands. In this paper we attempt to explain the restriction of spruce-fir forest to drainage bottoms by comparing fire frequency and the rate of secondary succession (i.e., the time required for development of a mature spruce-fir forest after destruction of an earlier forest) along a topographic gradient from moist ravines and valley bottoms to comparatively dry ridgetops and exposed slopes. Two hypotheses are tested: (1) fire is less frequent in drainage bottoms than on adjacent slopes and ridgetops, allowing the development and longer persistence of spruce-fir stands; and (2) secondary succession is more rapid in drainage bottoms, allowing maturation of spruce-fir forest during the interval between successive fires while adjacent uplands remain covered by seral lodgepole pine forests.

Although evidence of past fires in the Medicine Bow Mountains is common, the natural frequency and extent of fire in relation to topographic position is not known. One problem in obtaining this information is that the usual approach for studying fire history, based on dating fire scars on living relic trees (Arno and Sneek 1977), is of limited value in forests where the trees are so fire-susceptible that fire-scarred relics are rarely found. Fire-scarred spruce and fir were not seen anywhere in our study area, and scarred lodgepole pine were rare. Therefore we used an alternative (though less precise) approach which involves the

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² Present address: Department of Natural Science, Eastern Kentucky University, Richmond, Kentucky 40475 USA.

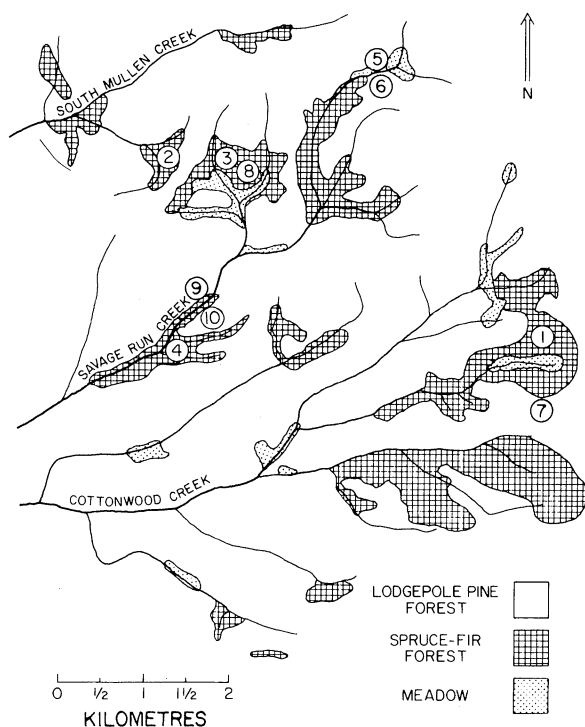


FIG. 1. Forest-type map of the 4500-ha upper Savage Run Watershed, showing the distribution of spruce-fir forests along drainage bottoms with lodgepole pine forests dominating the upland. Where pine forest is shown adjacent to a stream, the drainage bottom lies in a narrow valley with a thin band of spruce and fir, or supports a mixed riparian community containing elements of the spruce-fir, meadow, and pine communities. Circled numbers 1-4 indicate locations of stand pairs in which stand age was compared in valley bottom and adjacent upland stands; numbers 5-10 indicate stands in which the rate of succession was compared on different topographic sites (see text). Redrawn from United States Forest Service (1977).

comparison of stand ages. We assumed that if fire has been less frequent overall in drainage bottoms, then spruce-fir forests in ravines and valley bottoms should be generally much older than the pine forests on adjacent slopes and ridgetops; whereas if fire frequency has been about the same on all sites, then adjacent spruce-fir and pine forests should be of approximately the same age. Stand age in this context refers to the time since the last destructive, stand-replacing fire, not to the average age of the extant trees.

STUDY AREA AND METHODS

The study was conducted in the Savage Run Watershed, located on the western slopes of the Medicine Bow Mountains about 80 km west of Laramie, Wyoming (latitude 41°11'N, longitude 106°22'W). This 8500-ha natural area extends from the foothills into the subalpine zone and encompasses the only major undisturbed watershed in the Wyoming portion of the Medicine Bow Mountains. In 1978 the area was des-

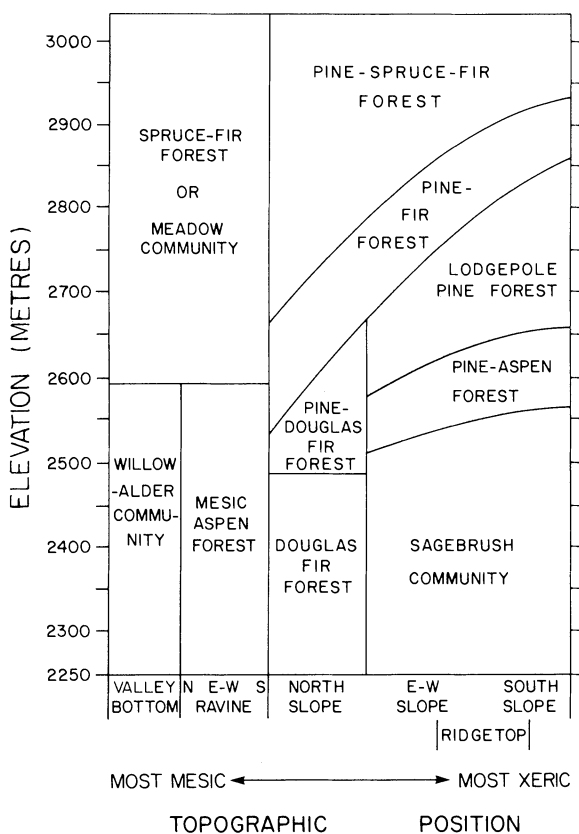


FIG. 2. Vegetation of the 8500-ha Savage Run Watershed in relation to elevation and topographic position. See Romme (1977) for descriptions of community types.

ignated the Savage Run Wilderness by the United States Congress. The major part of our study was conducted in the subalpine portion of the Watershed, an area of relatively gentle ridges and valleys covering about 4500 ha and lying between 2700-3000 m on metamorphic and granitic bedrock.

The vegetation of the Savage Run Wilderness is representative of foothill, montane, and lower subalpine portions of the Medicine Bow Mountains (Romme 1977). Most of the area is covered by nearly unbroken coniferous forest except for several meadows along streams and aspen or sagebrush communities at lower elevations. Lodgepole pine is a dominant over most of the area, with the codominant trees varying from Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *glauca* [Beissn.] Franco) or aspen (*Populus tremuloides* Michx.) at lower elevations to subalpine fir at intermediate elevations and subalpine fir and Engelmann spruce at higher elevations. On exposed sites at intermediate elevations lodgepole pine is the only well-represented tree species, even in older stands.

There have been few recent major fires in the Watershed, over 90% of the forest being >150 yr old and over 50% being >200 yr old (United States Forest Service 1977). Since 1946 seven lightning fires have oc-

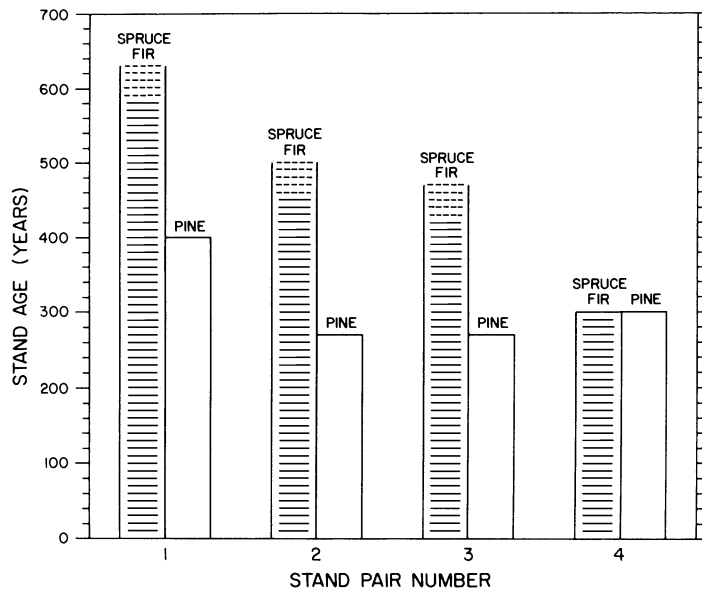


FIG. 3. Stand age in drainage-bottom spruce-fir forests and adjacent upland lodgepole pine forests (see Fig. 1 for locations of the four stand pairs). Stand age refers to the time since the last destructive fire. The solid horizontal lines in the spruce-fir forest columns extend to the age of the oldest tree sampled; where the stand is older than the extant dominants, dashed lines extend to an estimated minimum stand age (see text and Table 1). Stand pair 1 is at 2930 m elevation; pairs 2 and 3 are at 2870 m; and pair 4 is at 2680 m.

curred, all covering <4 ha when extinguished (United States Forest Service 1977 and *personal communication*). Current policy is to control all fires in the area.

Our study of the Savage Run Watershed began with an analysis of plant community composition, distribution, and successional status in relation to elevation and topographic gradients. Density, basal area, and frequency of trees (>10 cm dbh) and saplings (2–10 cm dbh) were estimated with the point-quarter distance method in 14 forest stands. In addition, visual estimates of species composition and successional status were obtained for an additional 71 stands. Each of the 85 stands was classified subjectively as one of 11 community types on the basis of dominant species, overall community structure (e.g., forest or shrubland), and habitat (riparian or upland). The 85 classified stands were then plotted on axes of elevation and topographic position, and lines were drawn to delineate approximate distributional boundaries of each community type (Fig. 2). The topographic position axis was constructed from observations on slope position and exposure of the 85 stands and it was arranged primarily to reflect soil moisture conditions. Stand age was estimated in 18 stands using increment cores.

To determine whether spruce-fir forests along drainages are generally older than the pine forests on adjacent slopes and ridgetops, four pairs of stands were selected for intensive study (labelled 1–4 in Fig. 1), each pair consisting of a mature spruce-fir forest in a

ravine or valley bottom plus the adjacent pine forest having a spruce and fir-dominated understory. In each stand 5–10 unsuppressed, dominant trees were aged with an increment corer as close to the base as possible. An estimate of the number of years necessary to grow to coring height (≈ 20 cm in most cases) was added to the number of rings on the core to arrive at tree age. This estimate of age at coring height was based on the width of the innermost rings, and ranged from 3 yr/20 cm height in trees with very wide rings (4–6 mm) to 20 yr/20 cm height in trees with very narrow rings (≤ 1 mm). These values were obtained by sampling several fast- and slow-growing saplings both at the base and at a height of 20 cm. In even-aged lodgepole pine stands (i.e., where the ages of most of the dominant canopy trees are within a 20–30 yr range) the age of the oldest tree sampled (excluding relics) was considered the age of the stand. Lodgepole pine is generally recognized as a species which invades following fire, forming even-aged stands.

Our estimates of stand age in the spruce-fir forests were based on two criteria: (1) ages of the dominant spruce, and (2) annual ring patterns. Age data were obtained from Engelmann spruce because this species lives upwards of 500 yr in this region, whereas subalpine fir rarely exceeds 300 yr (Oosting and Reed 1952). In a stand where the currently dominant spruce recolonized an open site after the last major fire, one would expect most of the dominant trees to be of about the same age, corresponding to the approximate stand age. Most would have relatively wide annual rings

TABLE 1. Ages and growth patterns of seven dominant spruce (*Picea engelmannii*) in a spruce-fir stand in which the time since the last destructive fire is greater than the age of the extant dominants (Stand 1 in Fig. 1). Very narrow rings, <1 mm; narrow rings, 1–2 mm; wide rings, 2–4 mm; very wide rings, 4–6 mm.

Tree number	dbh (cm)	Age	Annual ring pattern
1	65	585	Very narrow first 70 yr; narrow next 30 yr; very narrow thereafter.
2	53	435	Narrow first 60; wide next 30; very narrow thereafter.
3	58	375	Very narrow first 125; narrow thereafter.
4	53	370	Wide first 50, gradually diminishing; very narrow last 300.
5	50	360	Very narrow throughout.
6	58	265	Narrow throughout.
7	53	220	Narrow throughout.

near the center, indicating favorable initial growing conditions, with the rings gradually becoming narrower as the forest closed and competition became more intense. By contrast, trees that became established in a seral lodgepole pine forest or a spruce-fir forest would be of various ages and would have narrow annual rings from the early years of suppression. The rings might remain narrow throughout the life of the tree, or they might become wider during a period of release. The age of such a stand is impossible to estimate, but probably would be at least 50 yr older than the oldest spruce sampled, and may be many generations older.

There are, of course, many factors complicating the interpretation of annual ring patterns. Narrow annual rings during early years of growth may represent solarization (Ronco 1970), browsing (Black et al. 1969), or herbaceous competition (Stahelin 1943, Langenheim 1962) on an open site rather than suppression under a closed canopy; new seedlings in an old forest gap may grow rapidly for several years. In practice, however, we felt confident in judging which of the two ring patterns predominated in the stands that we studied.

Estimating the time required for development of

mature, upland spruce-fir forest was necessarily somewhat speculative because such forest presently is very rare in the Watershed. However, the fact that spruce and fir frequently dominate the understory in upland pine forests indicates that many sites are at least potentially capable of supporting spruce-fir forest. Where pine currently dominates the canopy but spruce and fir dominate the sapling stratum, we assumed that the time necessary for development of spruce-fir forest equals the average lifespan of lodgepole pine in this area (350–400 yr, based on our increment cores) plus the number of years necessary for maturation of the understory trees after death of the pine canopy (50–100 yr). Where pine as well as spruce and fir saplings are well-represented in the understory, we assumed that two or more successive pine generations would be well-represented in the canopy, thus prolonging the time required for development of mature spruce-fir forest by 200 yr or more. These time estimates may vary somewhat with site conditions in the Watershed, but they served to provide a time scale which seemed adequate for our objectives.

RESULTS

The results of the gradient analysis (Fig. 2) show the restriction of mature spruce-fir forests to drainage bottoms and the predominance of pine-dominated communities on upland sites. Lodgepole pine is the only dominant pine species in this area, although limber pine (*Pinus flexilis* James) and ponderosa pine (*P. ponderosa* Dougl. ex Laws.) do occur at lower elevations. Whipple (1975) described a similar elevational sequence of lodgepole pine-dominated communities ≈150 km to the south in Colorado (39°50'N), the major difference being that comparable communities occur in zones ≈200 m higher in his study area.

In three of the four pairs of stands in which stand age was compared, the spruce-fir forest in the valley bottom is older than the pine forest on adjacent slopes or ridgetops (Fig. 3). The ages and annual ring patterns in these spruce-fir stands show that the extant dominants probably germinated under an established canopy, the dominant spruce being all-aged (a 350-yr range) and most having grown slowly during the first 50–150 yr (Table 1). Many trees are >400–500 yr old,

TABLE 2. Ages and growth patterns of dominant spruce (*Picea engelmannii*) in a 300-yr-old spruce-fir forest (Stand 4 in Fig. 1). See Table 1 for ring width definition.

Tree number	dbh (cm)	Age	Annual ring pattern
1	65	300	Narrow first 55 yr; wide next 70 yr; narrow next 100 yr; very narrow thereafter.
2	65	295	Very wide first 160; narrow next 90; very narrow thereafter.
3	65	285	Wide first 125; narrow next 60; very narrow thereafter.
4	65	280	Narrow first 110; wide next 90; very narrow thereafter.
5	60	255	Narrow first 70; wide next 120; very narrow thereafter.
6	70	250	Wide first 100; narrow or very narrow thereafter.
7	70	225	Wide first 115; narrow next 45; very narrow thereafter.

indicating that these stands are at least 150–200 yr older than the surrounding upland pine forests. Thus at least some of the spruce-fir forests in ravines and valley bottoms escaped the fires that destroyed the forests on adjacent slopes and ridgetops 250–400 yr ago; apparently fires occur less frequently in the drainage bottoms than on the uplands.

Drainage bottoms evidently do burn occasionally, however. In a fourth pair of stands the spruce-fir forest and the adjacent pine forest are both approximately 300 yr old (Fig. 3). The age distribution and annual ring patterns of the dominant spruce in the spruce-fir forest show that they probably recolonized the site after a major disturbance, the trees being roughly even-aged and several having grown rapidly during the first 100–150 yr (Table 2).

Fig. 4 shows relative basal area (%) for trees and saplings of spruce, fir, and pine in two adjacent 270-yr-old stands at 2950 m elevation, one on a comparatively mesic north-facing slope and the other on a xeric south-facing slope (stands 5 and 6, Fig. 1). Large, old pines of a single age class (245–265 yr old) are a conspicuous component of the canopy in both stands, but the understories are quite different and indicate more rapid succession on the mesic site. Subalpine fir saplings dominate the understory on the south-facing slope, but with pine also well represented. In contrast, pine saplings were not encountered on the north slope, spruce and fir saplings having approximately equal basal area.

Data from other upland stands also suggest that a mature spruce-fir forest can develop more rapidly on more mesic sites. For example, two late successional stands were located, one on a ridgetop at 2930 m (stand 7, Fig. 1), the other on a lower slope at 2860 m (stand 8, Fig. 1), both approximately 400 yr old. The forest canopy of the ridgetop stand is still dominated by even-aged pine, although extensive mortality is beginning to occur, while the understory is dominated by fir with smaller amounts of spruce and pine (relative basal areas of sapling fir, spruce, and pine being 70%, 18%, and 12%, respectively). By contrast, the canopy of the comparably-aged lower slope stand is already dominated by moderate to large spruce and fir, with pine occurring as scattered large trees that appear to represent remnants of a former even-aged cohort. At lower elevations (2700–2850 m) spruce and fir are prominent in the understory on north-facing slopes, but are rare on the drier south-facing slopes (Fig. 2). For example, in a pair of stands at 2790 m (stands 9 and 10, Fig. 1), both >200 yr old, the relative basal areas of pine, spruce, and fir in the understory of the north-slope stand are 18%, 21%, and 61%, respectively, while in the adjacent south-slope stand spruce and fir of any size are rare. There is no evidence that a spruce-fir forest will ever develop on this latter site. At all elevations above ≈ 2550 m we found a greater abundance and size of spruce and fir on more mesic

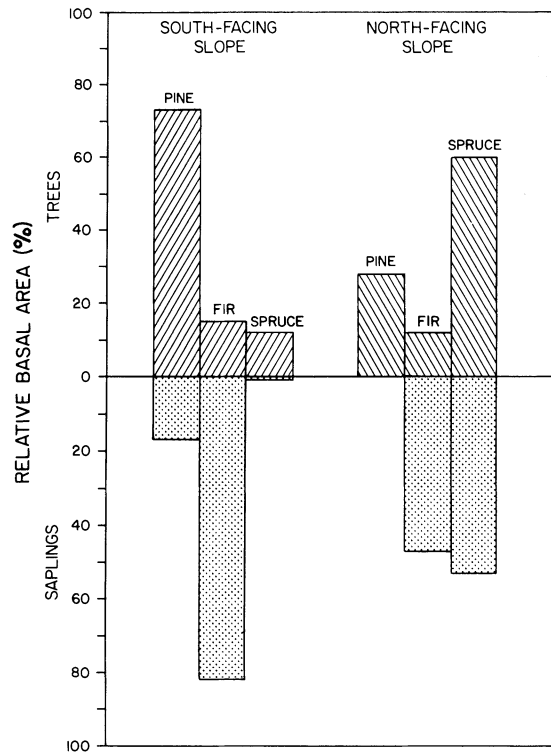


FIG. 4. Relative basal area (%) in two 270-yr-old lodgepole pine forest stands on adjacent north- and south-facing slopes at 2950 m elevation. Trees are stems > 10 cm dbh, saplings 2–10 cm dbh. Relative density and relative frequency show similar patterns.

sites (north-facing slopes and lower slope positions) than on nearby more xeric sites (south-facing slopes and ridgetops). Below 2550 m spruce and fir are generally absent from upland sites, although they still occur in a narrow band along streams in association with willows and alders (Fig. 2).

DISCUSSION

We hypothesized that upland spruce-fir forests are rare in the Savage Run Watershed because fires occur on the upland too frequently. This appears to be true even though there have been very few major fires in the Watershed for over 150 yr (United States Forest Service 1977). Apparently lodgepole pine forest persists on the upland not simply because fire is very frequent, but more important, because succession is very slow and fire usually recurs before spruce and fir replace lodgepole pine as the dominant species.

There is support for both of our hypotheses on why spruce-fir forests occur primarily in drainage bottoms. Fire is generally less frequent in drainage bottoms than on surrounding slopes and ridgetops; spruce-fir forests in ravines and valleys are frequently much older than adjacent pine forests. However, when fire does occur in a drainage bottom succession may be more direct and more rapid, a mature spruce-fir forest developing

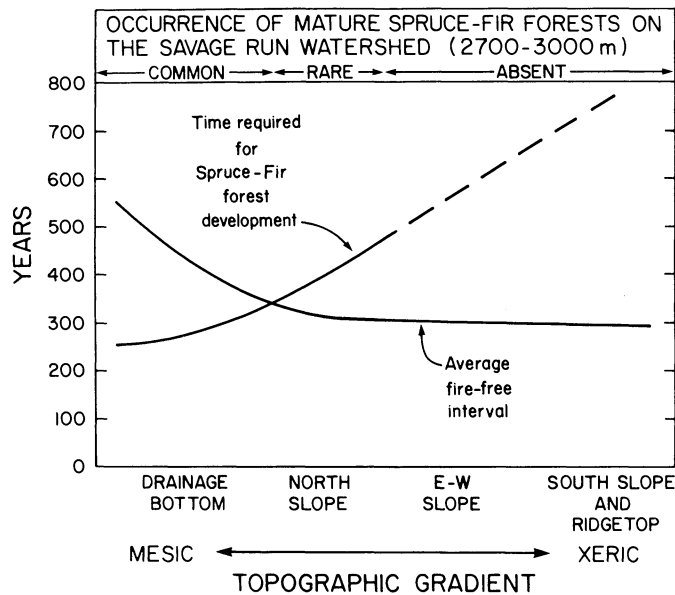


FIG. 5. Occurrence of mature spruce-fir forests, estimated mean fire-free interval, and estimated time required for development of mature spruce-fir forest along a topographic gradient in the Savage Run Watershed (2700–3000 m elevation). The dashed line indicates sites where spruce-fir forests probably never develop. Spruce-fir forests do occur on the upland at higher elevations (see text).

while adjacent uplands are still covered by pine-dominated successional stages.

There may be several reasons why drainage bottoms would be subjected to fewer fires, two major factors being the tendency of fire to burn uphill rather than downhill and the reduced probability of lightning strikes in low-lying areas (Brown and Davis 1973). The higher humidity and abundance of green herbaceous fuels that characterize drainage bottoms may further retard fire ignition and spread. Differences in the moisture content of fine, woody fuels may also be significant. Cooler night temperatures and higher relative humidity tend to reduce the amount of drying of these fuels in drainages compared to upland sites (Furman 1978); preliminary measurements in our study area indicate that the late summer moisture content of dead, woody material from 0–10 cm diameter is consistently higher by 2–5% in drainage bottoms compared to adjacent slopes and ridgetops (Romme 1977).

Successional patterns after fire also differ among various topographic sites. A mature spruce-fir forest probably can develop on a moist drainage site in as little as 200–300 yr, as indicated by the 300-yr-old stand described in Table 2. Most trees in this stand have grown slowly during the last 100 yr, indicating that they reached near-maximum size after only about 200 yr. On mesic upland sites, such as the north-facing slope referred to in Fig. 4, a mature spruce-fir forest probably develops after about 400 yr. This estimate is based on our observations that the lodgepole pine which dominate early stages of post-fire succession

rarely live longer than 350–400 yr in this area, with understory spruce and fir reaching large size and relatively high density by the time the pine canopy begins to deteriorate. On more xeric upland sites, such as the south-facing slope referred to in Fig. 4, development of a climax spruce-fir forest would require many centuries free from disturbance and probably rarely if ever occurs. These sites apparently are less favorable for spruce and fir establishment, many of the canopy gaps being filled by a second pine generation. The result is perpetuation of a mixed pine-fir-spruce forest. After several successive generations the forest might become dense enough finally to exclude pine, but it is unlikely that such xeric sites would escape fire long enough for this to occur. Therefore, as Whipple (1975) suggests, the climax or self-perpetuating vegetation type on more xeric sites appears to be a mixture of pine, fir, and spruce. With decreasing elevation spruce becomes less common on upland sites, leaving a mixed pine-fir forest (Fig. 2) which probably is a stable community type for the same reasons discussed above. Spruce and fir disappear on the most exposed sites at lower elevations (Fig. 2), leaving only lodgepole pine, the most drought-tolerant of the three species (Moir 1969, Whipple and Dix 1979).

The relationships between fire frequency, succession, and dominant community types along a topographic gradient are summarized in Fig. 5. The curve showing the time required for development of mature spruce-fir forest is based on the above discussion, with a dashed line indicating that spruce-fir forests probably

never develop on xeric sites (although they could develop theoretically). The curve showing average fire-free interval must be somewhat speculative because of the rarity of living fire-scarred trees in the area. Recent fire history studies in the northern Rocky Mountains (Arno 1980, Gabriel 1976, Sneek 1977, Tande 1979) indicate considerable geographic variability in the average fire-free interval of the subalpine zone, with values ranging from 22 to >150 yr. Fewer quantitative fire history studies have been done in the southern and central Rocky Mountains, but evidence suggests that fires there are less frequent. Clagg (1975) reports a low recent frequency of lightning fires in northern Colorado, $<8 \text{ fires} \cdot 4050 \text{ km}^{-2} \cdot \text{yr}^{-1}$, and estimates the average frequency of fires $>4 \text{ ha}$ prior to 1870 to be approximately $0.5 \text{ fires} \cdot 4050 \text{ km}^{-2} \cdot \text{yr}^{-1}$. Observations by D. G. Despain (*personal communication*) and our own data (Romme 1979) indicate that fuel conditions suitable for a second destructive burn may not develop for 300 or more yr after a fire in the upland subalpine forests of Yellowstone National Park. In several instances in this area, fires burning intensely in old, late-successional stands (350+ yr old) have failed to move into younger stands (up to 100 yr old) (Despain and Sellers 1977). Hendrickson (1972) estimated an average fire interval of 100–300 yr for lodgepole pine forest. Based on this information plus our stand-age data showing extensive fires 250–400 yr ago but few recent major fires in the Savage Run Watershed, we have adopted 300 yr as our current best estimate of mean fire-free interval on the upland, with a longer mean interval in drainage bottoms. It should be stressed that this estimate applies to individual stands, not to the Watershed. It is possible that one of the suppressed fires during the last 35 yr would have burned a larger area if not controlled. However, we believe that primarily older stands ($>300 \text{ yr}$) would have burned, and thus our 300-yr estimate would have remained unchanged. The qualitative relationships in Fig. 5 are to be emphasized, with the numerical data being tentative until additional fire history data can be obtained.

Although upland spruce-fir forests are rare within the elevational range of the Savage Run Watershed (2250–3000 m), extensive upland spruce-fir forests are found above 3000 m in the Medicine Bow Mountains (Stahelin 1943, Oosting and Reed 1952). These forests probably develop because of reduced fire frequency at higher elevations, absence of lodgepole pine as a seral species, or a combination of these factors.

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